



Macrofauna communities across a seascape of seagrass meadows: environmental drivers, biodiversity patterns and conservation implications

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Abstract

Similar to other coastal biogenic habitats (e.g. tidal marshes, kelp forests, mangroves and coral reefs), a key function of seagrass meadows is the enhancement of biodiversity. Variability at multiple spatial scales is a driver of biodiversity, but our understanding of the response of macrofauna communities to variability of seagrass meadows is limited. We examined the macrofauna community structure (abundance and biomass) and diversity patterns (α - and β -diversity) across a seascape gradient of eleven seagrass meadows differing in the number, composition and density of plant species. The variability of the macrobenthic communities was regulated by a combination of sedimentary (mainly for the infauna) and macrophyte (mainly for the epifauna) predictors. We demonstrate that the natural occurrence of drifting algae trapped in the aboveground complexity of the meadows benefits seagrass macrofauna. Seagrass-associated macrofauna showed a clear increase in abundance and α -diversity metrics with increasing habitat complexity attributes (i.e. shoot density, plant biomass and canopy height). Furthermore, partitioning of β -diversity (i.e. the variation of species composition between sites) implied the replacement of some species by others between sites (i.e. spatial turnover) instead of a process of species loss (or gain) from site to site (i.e. nestedness). Therefore, the enhancement of macrofauna diversity across an increasing gradient of seagrass complexity, and the dominance of the turnover component suggest that devoting conservation efforts on many different types of meadows, including the less diverse, should be a priority for coastal habitat-management.

Keywords Coastal habitats · α - and β -diversity · Benthic · Baltic Sea · Community dynamics

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Introduction

Seagrass meadows influence key coastal processes such as productivity, filtering, carbon sequestration, and food webs, turning these coastal habitats into one of the highest global economic assets among natural ecosystems (e.g. Boström et al. 2006a, b; McGlathery et al. 2007; Duarte et al. 2010; Fourqurean et al. 2012). In addition, seagrass provides food and shelter for numerous faunal organisms including a diverse array of macroinvertebrates (Hovel and Lipcius 2002; Boström et al. 2006a). Simultaneously, macrofauna communities are known to contribute to coastal ecosystem processes such as primary and secondary production, trophic transfer, and biogeochemical fluxes (e.g. Peterson and Heck 2001; Duarte et al. 2010; Lohrer et al. 2016; Rodil et al. 2020).

The macrofauna communities associated with seagrass meadows have been studied extensively, and clear evidence of macrofauna community variability has been documented at different spatial scales (e.g. Hovel and Lipcius 2002; Borg et al. 2010; Boström et al. 2011). Macrofauna communities, in terms of density, biomass and diversity, are generally positively affected by the presence of seagrass (Boström and Bonsdorff 1997; Boström et al. 2006b; Fredriksen et al. 2010; Lohrer et al. 2016). However, the majority of the studies investigating the impacts of seagrasses on benthic fauna diversity are based on comparative surveys between bare sand and seagrass vegetation, while seascape diversity comparisons of different types of seagrass communities across different locations are scarce (see Boström et al. 2006a, b). Furthermore, the majority of the biodiversity datasets are based on monoculture meadows that do not include the multispecific component of seagrass variability across spatial scales (e.g. Bell et al. 2001; Boström et al. 2006a, b; Lohrer et al. 2016). Seagrass meadows worldwide can contain a high diversity of aquatic plants, especially in tropical regions (Duarte 2000; Short et al. 2007). In the case of the Baltic Sea, the aquatic flora is represented by a diversity of meadows ranging from monospecific patches dominated by high-biomass species, such as *Zostera marina* and *Ruppia* spp, to a different mixture of limnic species (e.g. Kautsky 1988; Gustafsson and Norkko 2019). This rich range of plant biodiversity is known to influence coastal ecosystem functioning (Gustafsson and Boström 2011).

Seagrasses are among the most impacted environments on earth (Lotze et al. 2006; Waycott et al. 2009) affecting associated macrofaunal communities and coastal biodiversity (Airoldi et al. 2008). For instance, eutrophication affects coastal habitats worldwide through increasing proliferation of seasonal mats of ephemeral algae that inhibit the growth and survival of aquatic plants and associated communities (Norkko and Bonsdorff 1996; McGlathery 2001; Holmer et al. 2009; Gustafsson and Boström, 2011). The effects of drifting algal mats on coastal vegetation and faunal communities have been studied mainly through experimental manipulations and from the point of view of the deleterious effects of algal blooms under eutrophication (e.g. Holmquist 1997; Gustafsson and Boström 2014). However, natural occurrences of drifting algal mats can become an alternative habitat for mobile benthic invertebrates. High abundances of macroinvertebrates have been reported in sublittoral accumulations of drifting algae compared to bare sands and other vegetation communities (Holmquist 1997; Norkko et al. 2000; Råberg and Kautsky 2007). Many studies have tried to disentangle the roles of different environmental and macrophyte drivers on the variability of seagrass macrofauna. To our knowledge, no studies have tried to include the structuring community role of natural occurrences of algal mats associated with seagrass meadows.

The analysis of faunal diversity associated with any marine or terrestrial system is valuable because it allows for testing different hypotheses regarding the processes driving species distributions and maintaining biodiversity (e.g. Baselga 2010; de Juan et al. 2013). As biodiversity is inseparably tied to habitat diversity (e.g. Hewitt et al. 2005), the loss of structurally complex habitats such as seagrass meadows are expected to be a major threat to marine biodiversity, and consequently to coastal ecosystem functioning. Hence, knowledge of macrofauna diversity patterns across broad scales is important for better management decisions and conservation practices in marine habitats (Airolidi et al. 2008; de Juan et al. 2013). However, little is known about the effects of environmental drivers on the macrofauna community composition across multispecific seagrass meadows (Boström et al. 2006b). The need for broad scale comparisons of seagrass meadows with different characteristics is key to understanding the high variability of seagrass systems that is often seen in the coastal zone to deduce the biodiversity consequences of habitat loss. Here, we examine differences in macrofauna community and diversity patterns across eleven seagrass meadows differing in the number, composition and density of plant species. Our aims are (1) to determine the role of drifting algal mats typically associated with the seagrass meadows by means of partitioning the role of sedimentary (e.g. grain size and pigments) and macrophyte (e.g. shoot density, canopy height, macroalgal biomass) variables in describing the spatial variation of representative macrofaunal communities (i.e. epifauna and infauna), and (2) to explore the macrofauna diversity patterns (α - and β -diversity) across a spatial range of different seagrass meadows.

Material and methods

Location, study sites and sampling

We selected seagrass sites located across a 25-km distance along the southern shore of the Hanko Peninsula (Finland), close to Tvärminne Zoological Station (Fig. 1), following a gradient from East (i.e. inner sites) to West (i.e. outer sites). We sampled eleven seagrass meadows (<4 m depth) during peak biomass season (i.e. August–September 2017) using SCUBA diving (Fig. 1). One site, TS, was sampled at the beginning (early August, TS₀) and at the end (late September, TS_p) of the campaign to assess temporal variation (Table S1). Our study follows a spatially variable array of multispecific seagrass meadows dominated by the marine plant species *Z. marina* accompanied by several other limnic canopy-forming species. The sites were chosen based on their position along the peninsula, and a priori knowledge of species-rich plant meadows and macrophyte abundance occurring at the sites (Gustafsson and Norkko 2019).

At each site, we sampled a circular-shaped seafloor area of approximately 80 m² divided into eight equal 45° direction wedge sectors using transect lines (5 m-long per direction, 10 m Ø) for diving orientation (see Fig. S1). Two different types of benthic samples (i.e. quadrat and corer) were randomly taken per sector and site (16 total samples per site) to obtain samples of the main benthic community components. Hence, eight of the samples were collected within the inner area (0–3 m) of the circle, and eight samples were collected within the outer area (3–5 m) of the circle (Fig. S1). For each quadrat sample, we harvested all the vegetation and associated epifauna by gently enclosing all plants within a quadrat frame (25 cm×25 cm, n=16) into netbags. Benthic cores (Ø=5 cm, 15 cm deep) for macroinfauna were also taken at each

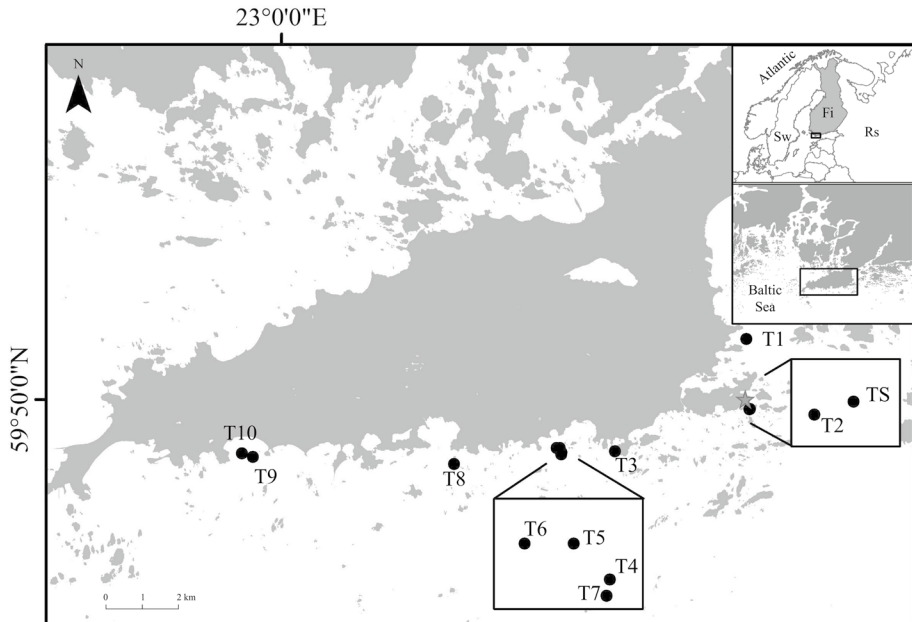


Fig. 1 Map of the study sites (star symbol is the location of Tvärminne Zoological Station) following a gradient from East (i.e. inner sites: T₁, T₂, T₃) to West (i.e. outer sites: T₉ and T₁₀) along the Hango peninsula in the Baltic Sea Archipelago (SW Finland)

site ($n=16$). Six random sediment samples were taken (3 inner+3 outer samples; Fig. S1) using 100 mL-syringes ($\varnothing=3.5$ cm, 10 cm deep) for organic matter and pigments (surface sediment, 1 cm layer), and grain size (the rest of the sediment). This protocol ensured that a major representation of the key biodiversity components across sites were sampled (Rodil et al. 2019).

Sedimentary characterization

For the grain size samples, large shell fragments were removed and the samples were treated with hydrogen peroxide (H_2O_2 , 6%) to dissolve organic material, then they were sieved (<63 , 63, 125, 250, 500, 1000 and 2000 μm), the percent dry weight of each fraction measured and the mean grain size (μm ; M_G) was calculated using GRADIS-TAT (Blott and Pye 2001). Homogenized surface sediment (0–1 cm) was analysed for organic material (OM, %) as loss on ignition (3 h, 500 °C). Sediment surface subsamples (~0.5 g) were placed into centrifuge tubes and 10 ml of 90% acetone was added to extract pigments from the sediment. Tubes were stored at 4 °C in darkness for 24 h and shaken periodically. Prior to analyses, the tubes were centrifuged at 3.000 rpm for 10 min at 20 °C to ensure that absorption at 750 nm was <0.005 . The supernatant (3 ml) was analysed in a spectrophotometer (Shimadzu UV–Vis model) before and after acidification with 2 drops (100 μl) of 1 N HCl to determine chlorophyll *a* (chl *a*) and phaeopigments (phaeo), respectively ($\mu\text{g g}^{-1}$).

Macrobenthic community characterization

All plant species were identified, and shoot density (hereafter, shootD) was measured by counting all shoots from the net-bags. Vegetation was divided into aboveground (AG, shoots) and belowground (BG, rhizomes + roots) samples, and dry mass (DM) was estimated (60 °C, 48 h). The maximum vegetative height (H_{\max}) of all the plant species was determined by measuring the tallest shoot from the top of the plant to where the shoot is attached to its rhizome in each plot, and the community-weighted average height (cm) was calculated (Gustafsson and Norkko 2019). Ephemeral algae associated to the aquatic plants were gently separated from the plant samples, identified and DM was estimated (60 °C, 48 h). Macrophyte-associated epifauna was sorted, identified and counted (ind m^{-2}). All the sediment from the benthic cores was sieved (0.5 mm); macroinfauna was sorted, identified and counted (ind m^{-2}). All shell-less invertebrates (polychaetes, crustaceans and others) were blot wet weighed (accuracy of 0.0001 g). The length (maximum anterior–posterior axis) of molluscs and gastropods was measured with a Vernier calliper (accuracy of 0.01 mm). Biometric conversion factors for invertebrates of the Baltic Sea (Rumohr et al. 1987) were used to obtain biomass information for all the species (ash free DM, AFDM g m^{-2}).

Macrofauna diversity metrics: α - and β -diversity

We used a combination of diversity metrics to describe the complexity of the macrofauna communities with respect to the number and abundance of the main taxa across sites (i.e. α -diversity). Species richness (SR), defined as the mean number of taxa per site, and evenness of distribution of individuals among taxa expressed by the Pielou index (J') were calculated. Species diversity measured with the Shannon-Wiener \log_e based index (H') and with the Simpson index ($1-\lambda$) was also calculated. We used beta diversity (β) as a multiple-site similarity measurement independent of patterns of richness to examine the variation in macrofaunal species composition across sites taking into account the identities of all species (Baselga 2010). We decomposed the β -diversity into nestedness-resultant (β_{nes}) and Simpson pairwise (β_{sim}) dissimilarities. The β_{sim} is a measure of turnover or the replacement of species between sites that reflects the replacement of some species by others, whereas β_{nes} implies a process of species loss (Baselga 2010). As β -diversity quantifies the change in species across sites, it is central to a wide array of ecological topics related to the processes driving species distributions and biodiversity (McKnight et al. 2007; Baselga 2010).

Statistical analysis

The distribution of sedimentary and macrophyte variables were examined (Draftsman plot routine and `rcorr` function in R) to assess skewness, outliers and correlations (Table S2). All multivariate analyses were performed using PRIMER7 (Clarke and Gorley 2015). Non-metric multidimensional scaling (nMDS) of distances among centroids based on a Euclidean resemblance matrix (log-transformed and normalized data) was used to visualize multivariate sedimentary patterns (4999 permutations). The discrimination of the sedimentary characteristics across sites was further tested with one-way analysis of similarity (ANOSIM). A principal component analysis (PCA) was used to

define the relative importance of different sedimentary variables determining the distribution of sites. The BEST analysis based on site sediment data (Euclidean dissimilarities) was performed to confirm suites of sedimentary variables that best determine the distribution of sites. A second PCA was used to examine the spatial distribution of shootD, plant biomass and plant species (4th-root transformed) across sites. We visualized multivariate patterns of the macrofauna using a nMDS of distances among centroids based on Bray–Curtis resemblance matrices, followed by ANOSIM for the discrimination of macrofauna assemblages (i.e. taxa-specific abundance; 4th-root transformed) across sites. The macrofauna taxa that mostly contributed to the similarity among sites were identified using SIMPER analysis. Calculations for macrofauna α -diversity indices (i.e. SR, J', H' and $1-\lambda$) were performed using the DIVERSE function.

Non-parametric multivariate analyses of variance (PERMANOVA) were run separately to detect significant changes in the abundance, biomass, number of taxa and diversity of the aquatic plants, associated ephemeral algae and macrofauna (epifauna and infauna) across sites (random factor, unrestricted permutation of raw data, Type III SS). We calculated distance resemblance matrices using Euclidean dissimilarity measures based on transformed data using 4999 permutations.

To ascertain how much of the overall change (i.e. variance partitioning) in the composition of the macrofauna across sites can be explained by the sedimentary and macrophyte (i.e. aquatic plants and macroalgae) characteristics (log-transformed predictor variables), distance-based linear models (DistLM) were performed (4999 permutations). Bray–Curtis (taxa-specific abundance) and Euclidean (abundance, AFDM, diversity metrics) similarity matrices were constructed after transforming the data. DistLM were fitted using the stepwise selection procedure and R^2 criteria. Distance-based redundancy analysis (dbRDA) was applied to visualize the position of the sites according to the macrofauna assemblages fitted to the significant predictor variables.

We aim to establish links between the macrofauna community structure and diversity components (i.e. abundance, biomass and α -diversity metrics) and the spatial distribution of the sites following a gradient of increasing shoot density. Hence, we used regression-based analysis for each response variable to estimate the average contribution of shoot density to the average macrofauna community variables across sites (SIGMAPLOT 14.0).

We assessed differences in species assemblages across all meadow sites by examining total β -diversity (Sørensen based multiple-site dissimilarity; β_{sor}), spatial turnover (Simpson-based multiple-site dissimilarity; β_{sim}) and nestedness (nestedness-resultant multiple-site dissimilarity (β_{nes} , which is calculated: $\beta_{\text{nes}} = \beta_{\text{sor}} - \beta_{\text{sim}}$) components. We compiled a presence/absence matrix for the species occurring in each site and we used average linkage cluster analysis to visualize relationships among sites. Analyses were carried out in R 3.6.1 (R Core Team 2020) using the functions within the “betapart” package (Baselga and Orme 2012; Baselga et al. 2018).

Results

Sedimentary characteristics across a seascape gradient of seagrass meadows

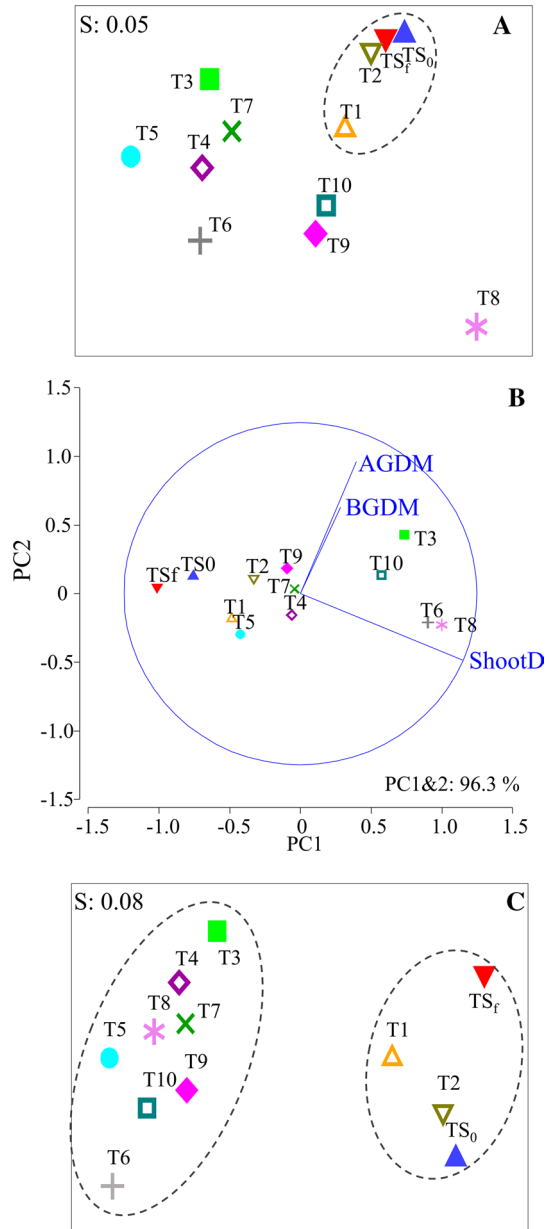
The nMDS ordination of the sedimentary characteristics indicated a separation of the different sites (ANOSIM; $R^2 = 0.630$; $p < 0.001$) along the spatial gradient (Fig. 1; Fig. 2a). A group of sites located in the inner most part of the study area clustered together compared

Table 1 Results of variation partitioning analysis (DistLM, sequential test) quantifying the sequential effects (step-wise selection, 4999 permutations) of the specific contribution of the macrophyte community attributes and the sedimentary predictors (log-transformed) on the macrofauna community across seagrass sites

Macrofauna community	Source	Macrophyte predictors				Sedimentary predictors				ΣR^2
		Algae	Chorda	AGDM	BGDM	H _{max}	Chla	Phaeo	M _G	
Abundance _{epifauna}	R ²	0.342	–	0.084	–	–	–	–	–	0.456
	SS	75.9	–	18.7	–	–	–	–	–	6.7
	pseudo-F	98.6***	–	27.8***	–	–	–	–	–	10.5**
Abundance _{infauna}	R ²	–	0.052	–	0.026	–	–	0.042	0.148	0.282
	SS	–	6.0	–	3.1	–	–	4.90	17.1	1.6
	pseudo-F	–	12.3**	–	6.7*	–	–	10.5**	32.8***	3.7*
AFDM _{epifauna}	R ²	0.405	–	0.017	–	–	–	0.056	–	0.478
	SS	14.7	–	0.60	–	–	–	2.04	–	–
	pseudo-F	129.2***	–	5.96*	–	–	–	19.7***	–	–
AFDM _{infauna}	R ²	0.054	0.074	–	0.043	–	–	0.079	0.034	0.284
	SS	6.6	8.9	–	5.3	–	–	9.5	4.1	–
	pseudo-F	11.4**	16.7***	–	8.6**	–	–	19.6***	8.9**	–
Number of taxa	R ²	0.238	–	0.189	–	0.04	–	–	0.058	0.557
	SS	425.7	–	338.0	–	72.4	–	–	104	56.7
	pseudo-F	83.8***	–	44.2***	–	9.9**	–	–	24.3***	11.8**
H'	R ²	0.165	–	0.057	–	0.050	0.060	–	–	0.332
	SS	2.9	–	0.99	–	0.88	1.1	–	–	–
	pseudo-F	42.7***	–	11.4***	–	10.7**	16.9***	–	–	–
Assemblage	R ²	0.014	0.011	0.019	–	0.011	–	0.192	0.066	0.340
	SS	3172	2571	4216	–	2511	–	43,583	14,941	6122
	pseudo-F	3.8***	3.1**	5.0***	–	3.1**	–	45.2***	16.8***	7.1***
Mean R ²		0.203	0.046	0.073	0.035	0.034	0.060	0.092	0.077	0.390
± SE		0.063	0.018	0.032	0.009	0.012	–	0.034	0.025	0.040

Significant results in italics (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$), and total R^2 in bold (see Fig. 8)

Fig. 2 Multivariate analyses: **A** Non-metric multidimensional scaling (nMDS) of distances among centroids based on the Euclidean measure of the sedimentary variables, **B** PCA showing the spatial distribution of the seagrass sites according to the average macrophyte descriptors (i.e. above- and below- ground dry mass and shoot density), and **C** nMDS of distances among centroids based on the Bray–Curtis measure of the macrofauna community abundance



to the rest of the sites ($R^2=0.335$; $p<0.001$) (Fig. 2a). The distribution of sites was defined (BEST correlation=0.746) by grain size, pigments and organic matter. Sites showed sediments dominated by grain sizes between 125 and 500 μm (Table S3; Fig. S2). In general, there is a grain size distribution linked to the location of the sites, with finer sediments in the inner sites (i.e. TS, T₁ and T₂) (Fig. 2; Fig. S3). In general, there was higher organic matter and pigments in the three inner sites (Fig. 2; Fig. S3).

Macrophyte characteristics across a seascape gradient of seagrass meadows

The seagrass meadows showed a spatial gradient related to their shootD and biomass (Fig. 2B). The first two axes of the PCA explained 96.3% of the variation in sites, with shootD contributing mainly to the first axis ($PC1=0.921$) (Fig. 2B). The main macrophyte characteristics showed significant changes across sites (Tables S4). We recorded the lowest shootD at site TS and the maximum shootD at sites T_6 and T_8 (> 1000 shoots m^{-2}) (Fig. 3A; Table S5). We recorded the lowest biomass (i.e. total DM) at site T_5 and the highest biomass at site T_3 (Fig. 3B–D; Table S5). Canopy height (H_{max}) did not show any trend across the spatial gradient (Fig. 3E; Table S5). We collected 9 plant species across all

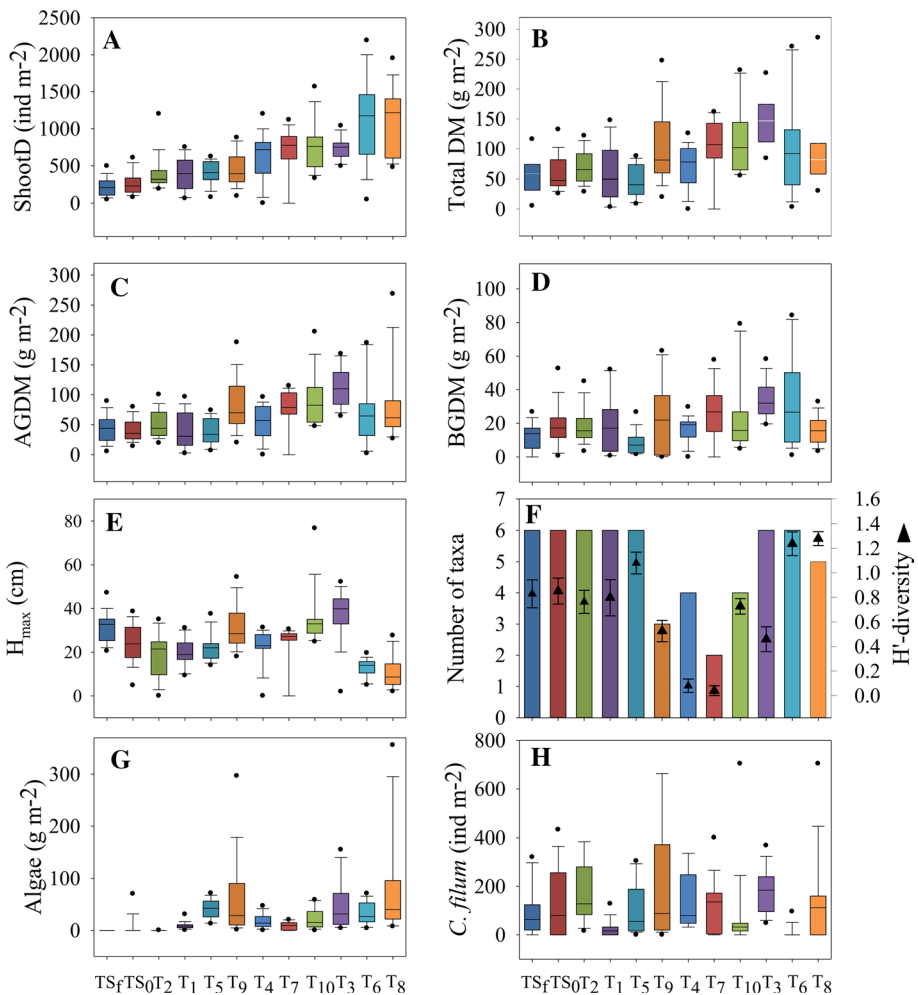


Fig. 3 Macrophyte community descriptors (mean \pm se) following a spatial gradient of increasing shoot density (see Fig. 2B). **A** Shoot density (shootD), **B** total dry mass (DM), **C** above- and **D** below- ground dry mass (AGDM and BGDM), **E** canopy height (H_{max}), **F** number of taxa and Shannon-Wiener \log_e based diversity index (H'), **G** algal biomass, and **H** the abundance of *Chorda filum*

sites, ranging from 2 to 6 at individual sites (Fig. 3F; Tables S5). Four dominant species, in terms of density and biomass (i.e. *Z. marina*, *S. pectinata*, *R. maritima* and *Zannichellia* spp), explained 67% (PCA1&2) of the plant distribution across sites (Fig. 4; Table S6; Fig. S4). We recorded the lowest diversity (H') at site T_7 (dominated entirely by *Z. marina*) and the highest H' at sites T_6 and T_8 (Fig. 3F; Fig. 4; Tables S5–S6).

The algal mat was a conglomerate of several drift-algal species of mainly filamentous algae (Table S7). The algal biomass changed significantly across sites (Fig. 3G; Table S4). There were significant correlations between algal biomass and some of the aquatic plant characteristics (i.e. shootD and AGDM; Table S2). The lowest algal biomass was recorded at TS, and the highest biomass was recorded at T_8 (Fig. 3G; Table S7). Fragments of detached rocky-shore perennial macroalgal species such as *Fucus vesiculosus* and *Furcellaria lumbricallis* were recorded within the algal mats (Table S7). The annual macroalgal

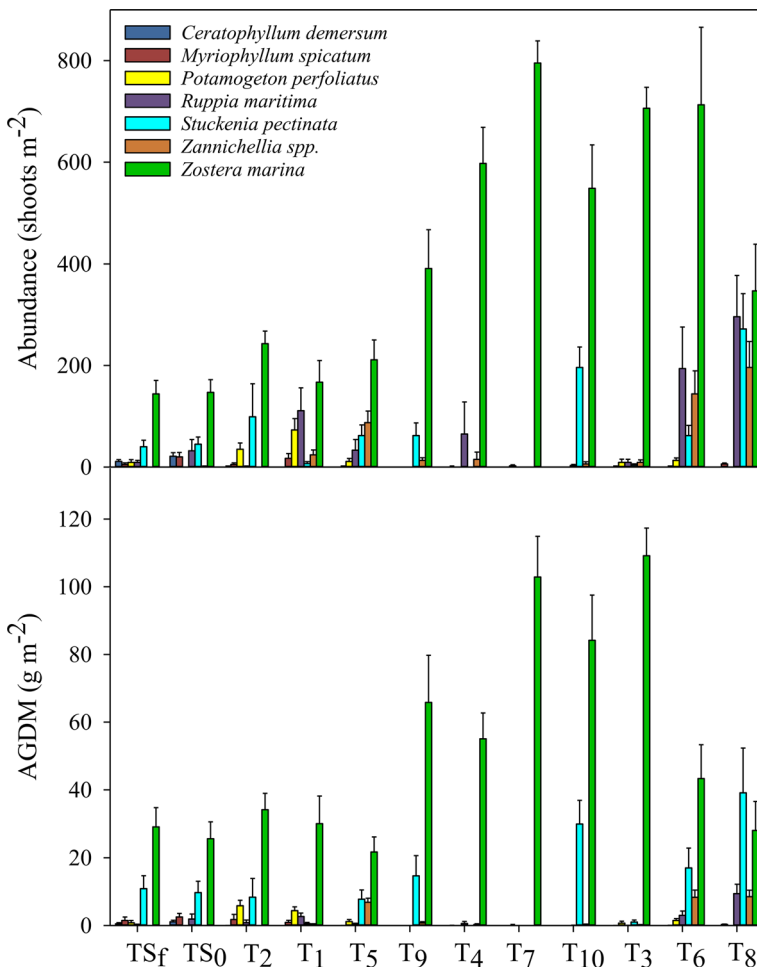


Fig. 4 Abundance and above-ground (mean \pm se) dry mass of the main plant species across all the seagrass meadow sites following a spatial gradient of increasing shoot density (see Fig. 2B)

species *Chorda filum* was abundant across sites (Fig. 3H; Table S6–S7), and it was significantly correlated with AGDM and H_{\max} (Table S2).

Macrofaunal community biodiversity across a seascape gradient of seagrass meadows

The total number of macroinvertebrate taxa across sites ranged from 19 to 25 (Table S8). We recorded a total of 22 marine taxa (11 crustaceans, 9 molluscs and 2 polychaetes) and 9 other taxa belonging to other groups (Table S9). SIMPER identified the species that typified each site (Table S10). The largest dissimilarities in macrofauna composition occurred between inner (i.e. TS, T_1 and T_2) and outer sites (Table S11). The taxa contributing the most to the similarity in the inner sites (70% cut-off) were molluscs (e.g. gastropod *Perin-gia ulvae*), polychaetes (e.g. *Marenzelleria* spp) and insect larvae *Chironomus* spp (Tables S9–S10). Crustaceans were not dominant at the inner sites (Table S10). Taxa dissimilarities among sites were related to the dominant presence of grazers such as crustaceans (e.g. *Idotea* spp and *Gammarus* spp) and gastropods (e.g. *T. fluviatilis* and *P. peregra*), and the omnivorous polychaete *H. diversicolor* at the outer sites (Table S9–S10).

The α -diversity metrics, including the mean number of taxa (SR), Shannon (H'), and Simpson ($1-\lambda$) increased significantly across sites following a gradient of increasing shootD (Fig. 5A–D; Table S12) and plant biomass (Fig. S5). The results showed that β -diversity ($\beta_{\text{sor}}=0.45$) was mainly due to the replacement of species ($\beta_{\text{sim}}=0.34$; i.e. turnover) rather

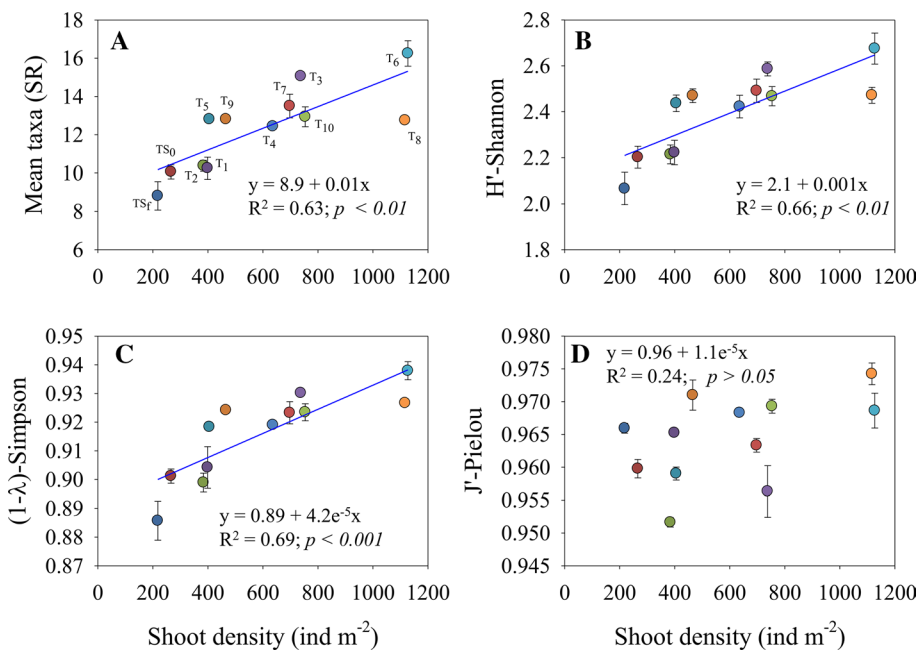


Fig. 5 Macrofauna community diversity (i.e. α -diversity; mean \pm se) increased significantly ($p < 0.001$) across sites following a spatial gradient of increasing shoot density (see Fig. 2B): **A** Mean number of taxa, **B** Shannon–Wiener log_e based index, **C** Simpson index, and **D** Pielou evenness index. Sites were labelled in (A) for reference

than species loss ($\beta_{\text{nes}}=0.11$; i.e. nestedness) across sites (Fig. 6A). The pairwise analysis allows the identification of patterns of dissimilarity across sites derived from the dominant turnover-resultant dissimilarity (Fig. 6B). Hence, pairwise β_{sim} -based cluster analysis grouped sites according to the inner-outer location to which they belonged (Fig. 6B), and those sites with the highest (T_6) and the lowest (TS_0) macrofauna diversity were grouped separately (Fig. 6B; Table S8).

The nMDS ordination of the macrofauna assemblages indicated a separation of the different sites ($R^2=0.673$; $p<0.001$) along the spatial gradient (Fig. 2C). However, two significant clusters were observed ($R^2=0.985$; $p<0.001$) (Fig. 2C); i.e. the inner sites (TS_{0-f} , T_1 and T_2) and the outer sites (T_3 – T_{10}). We found significant differences in macrofauna abundance and AFDM across sites (Table S12). In general, the inner sites (i.e. TS_0 , TS_f and T_1) showed the lowest macrofauna abundance and AFDM (Fig. 7A–B; Table S8). There was a rapid and significant increase in the abundance and AFDM across sites following a gradient of increasing shoot density (Fig. 7A–B), especially for the infauna (7C–D) compared to the epifauna (7E–F). Total macrofauna (and infauna) abundance and AFDM decreased significantly (i.e. quadratic regression) with the highest shoot densities (>1000 shoots m^{-2}) (Fig. 7A–D), whereas epifauna increased constantly (Fig. 7E–F). However, infauna showed higher abundance and AFDM compared to epifauna at any given site (Fig. 7; Table S8).

Partitioning the role of environmental drivers on macrofauna community variation

There was a significant association between epifauna (abundance and AFDM) and algal biomass (DistLM model explained 34.2 and 40.5% variation, respectively) and AGDM (8.4 and 1.7%) (Table 1; Fig. S6A). A significant part of the observed variation in macroinfauna abundance and AFDM was mainly explained by sedimentary predictors (20.4 and 11.3%, respectively), including phaeopigments and grain size (Table 1; Fig. S6A), and by macrophyte predictors (7.8 and 17.1%) including drifting algae, abundance of *C. filum* and BGDM (Table 1; Fig. S6A). The number of taxa and H' -diversity were significantly

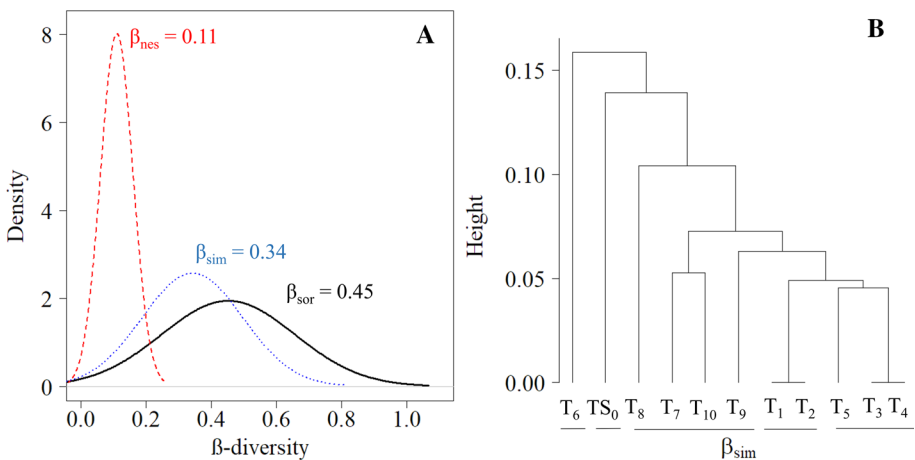


Fig. 6 **A** Partitioning of β -diversity (β_{sor} , solid line) into turnover (β_{sim}) and nestedness-resultant dissimilarity β_{nes} for eleven seagrass meadow sites (31 macroinvertebrate species, Table S9), and **B** clustering using average linkage of the β_{sim} component across sites

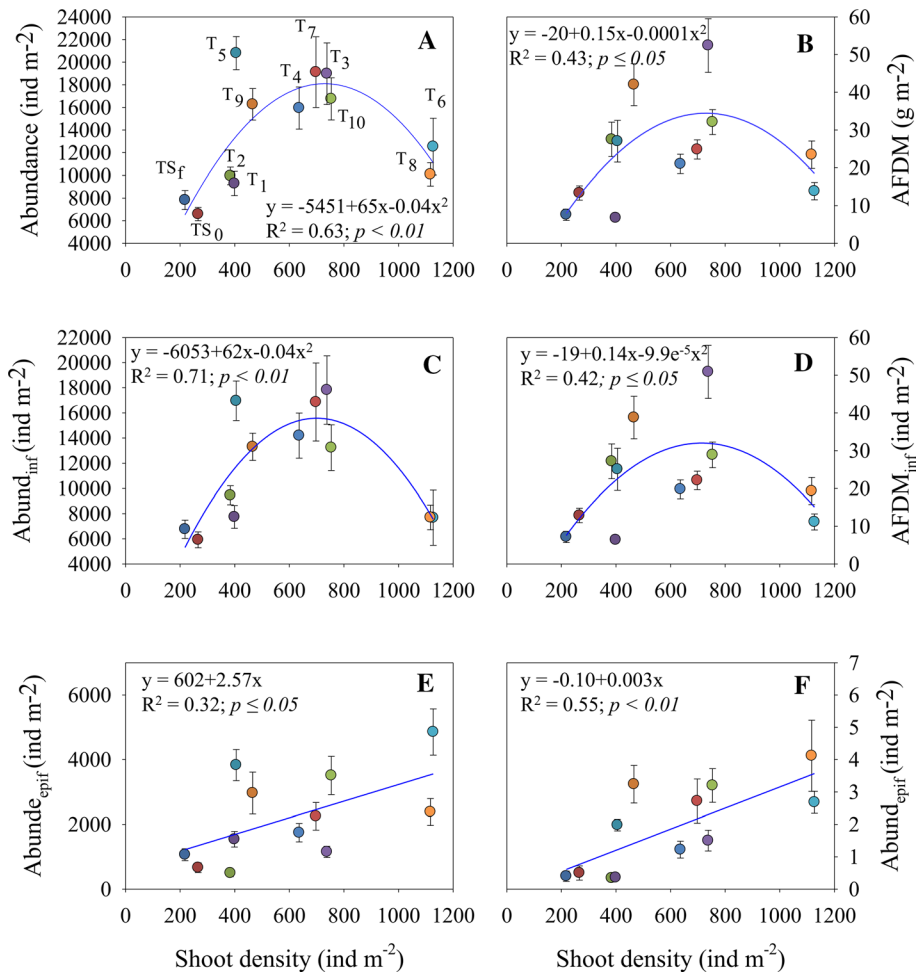


Fig. 7 Plots showing the significant increase ($p \leq 0.05$) of macrofauna community (mean \pm se) abundance (A), ash free dry mass (B), and macroinfauna and epifauna abundance (C and E) and ash free dry mass (D and F) across sites following a spatial gradient of shoot density (see Fig. 2B). Sites were labelled in (A) for reference

associated with algal biomass (23.8 and 16.5%, respectively) and to AGDM (18.9 and 5.7%) (Table 1; Fig. S6A). On average, model variation including all macrofauna descriptors was mainly explained by macrophyte drivers (39%), especially by algal biomass (20.3%), followed by environmental drivers (25.8%) (Table 1; Fig. S6B).

A significant part of the observed variation in the macrofauna assemblages (i.e. taxa-specific abundance) was explained by sedimentary predictors (28.5%), including phaeopigments and grain size, and macrophyte predictors (5.5%), including algal biomass (Table 1; Fig. S6A). The first 2 dbRDA axes captured most of the salient patterns in the fitted model with 82% of the variability, and nearly 28% of the total variation in the data cloud (Fig. 8). The ordination plot showed a separation of inner and outer sites, the former being associated with high values of phaeopigments and the latter more associated with algal biomass, plant AGDM and M_G (Fig. 8).

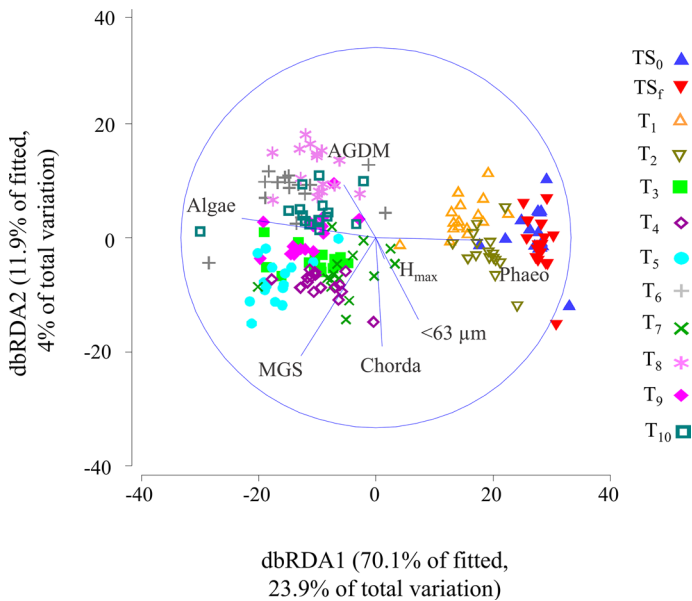


Fig. 8 dbRDA ordination for the main environmental predictors (i.e. phaeopigments: phaeo, mean grain size: MGS, < 63 μm , seagrass above- and below- ground dry mass: AGDM and BGDM, canopy height: H_{max} , filamentous algal biomass: algae and the abundance of *Chorda filum*: Chorda) and the macrofauna assemblages across seagrass sites

Discussion

Our study demonstrates that the diversity of the seagrass-associated macrofauna community was clearly promoted across a spatial gradient of increasing aquatic plant complexity. We also show that the variability of the macrofauna community across a seascape of multispecific seagrass meadows was determined by a combination of environmental (mainly infauna) and macrophyte (mainly epifauna) drivers, including the presence of natural occurring ephemeral algae.

Sediment and macrophyte characteristics across a seascape of seagrass meadows

There was a clear separation between sites located in the most inner and sheltered area (i.e. T_1 , T_2 and TS) with higher sedimentary organic content, pigments, and finer sediments than the more exposed outer sites. However, the outer sites showed a high variability in the sedimentary conditions, probably reflecting differences in the patch-size of the seagrass meadows since large patches may enhance the deposition of fine/organic sediments more than small patches, potentially influencing the associated macrofauna community (Frost et al. 1999; Bowden et al. 2001).

There was a clear distribution of the sites according to a spatial gradient of increasing plant complexity (shootD and biomass). The inner sites exhibited lower shootD and biomass compared to the rest of the sites, likely related to the site-specific sheltered conditions and sedimentary characteristics. Plant diversity, as represented by the Shannon-Weaver

index (H'), was within the expected range of species diversity (0–1.5) of seagrass communities (Duarte 2000). There was no significant relationship between shoot density (or biomass) and plant diversity (both, number of species and Shannon- H'), thus the highest plant diversity was found at contrasting sites with both low and high plant densities and demonstrates the high ecological variability of the meadows.

Macrofauna diversity across a seascape of seagrass meadows and conservation implications

Seagrass showed a positive influence on macrofauna abundance and diversity, in line with previous observations (e.g. Hovel and Lipcius 2002; Boström et al. 2011). Most of the studies have demonstrated that monoculture seagrass shows significantly greater abundance, richness and diversity of fauna than neighbouring unvegetated areas (Boström and Bonsdorff 1997; Mattila et al. 1999; Boyé et al. 2017). The few studies focusing on the macrofauna relationships across an array of seagrass meadows with different densities and species composition indicated that macrofaunal taxon richness tends to increase with increasing plant richness (Gustafsson and Boström 2011). Here, we describe the complexity of the seagrass macrofauna communities with respect to richness (i.e. number of taxonomic groups) and evenness (i.e. distribution of abundances of the groups) using a large array of α -diversity indices to provide greater insight into the species interactions of the habitat. All the macrofauna community variables and α -diversity metrics increased with the gradient of seagrass density and biomass, highlighting the importance of seagrasses for the diversity of macrofauna. To our knowledge, this is the first study showing that an increase in the complexity across seagrass meadows benefits the macrofauna community diversity. This is important since macrofauna communities in coastal areas of the Baltic Sea are generally abundant, but low in diversity (Gogina and Zettler 2010).

A broader picture of how seagrass influences associated biodiversity requires complementing the community assessments traditionally based on the local diversity (i.e. α -diversity) with the spatial differentiation of their communities (i.e. β -diversity) (Airaldi et al. 2008; Boyé et al. 2017). Ecologists often distinguish between two patterns of β -diversity, termed 'turnover' and 'nestedness' (see Baselga 2010 and references therein). Nestedness occurs when sites with a low diversity are subsets of sites with high diversity, thus species present at one site are absent at another, reflecting species loss (or gain) as a result of any ecological process that promotes the disaggregation of biological communities (e.g. ordered extinctions or colonizations along gradients, or from spatial patterns of decreasing resource or habitat availability). Species turnover implies the replacement of some species by others a consequence of environmental as well as spatial and historical differences among sites. This partitioning is key for an understanding of the ecological processes behind the spatial variation of the community biodiversity, for protecting regional diversity and can assist in conservation planning (Baselga 2010; Socolar et al. 2016).

In our study, β -diversity partitioning showed that β_{sim} was the dominant component, suggesting species sorting by environmental or dispersal processes rather than by ordered extinction and colonization patterns (Si et al. 2016; Soininen et al. 2017). This is a typical finding across a set of local communities, whereas biogeographical studies focusing on large-scale assemblages often find a considerable nestedness component (Baselga 2010; Soininen et al. 2017). The number of studies investigating the nestedness and turnover components of β -diversity has increased substantially, though the conservation implications have been mainly limited to terrestrial habitats (Socolar et al. 2016; Soininen et al.

2017). The distinction between the two components of β -diversity has been previously shown to be important for habitat-management planning, because nestedness and spatial turnover patterns require opposite conservation strategies (Baselga 2010). Nestedness suggests that conservation should target the richest sites, whereas turnover would prioritize conservation of multiple sites (Baselga 2010). Therefore, the dominant turnover component in our study suggests devoting coastal conservation efforts to a large number of different meadows, even when some individual sites are not particularly diverse.

Partitioning the role of seagrass-associated drivers on macrofauna community

Sediment (i.e. grain size and pigments) and seagrass (e.g. plant biomass and canopy height) variables explained a proportion of the macrofauna variability (total average of 25.8 and 14.1%, respectively). Granulometry is known to explain a significant part of the macrofauna variability, and it generally reflects the depositional and erosional nature of the study locations (Boström et al. 2006a; Boyé et al. 2017). Chlorophyll *a*, as a surrogate of microphytobenthos, can show differences between seagrasses mainly related to light intensity (among other variables such as depth and turbidity), thus it is expected that lower seagrass density (e.g. inner sites *versus* outer sites) results in higher production of microphytobenthos (Bianchi et al. 1988; Paula 2001). Phaeopigments are degradation products strongly influenced by seagrass detritus production and grazing activity (e.g. Bianchi et al. 1988; Paula et al. 2001). Above and belowground DM and canopy height are seagrass complexity attributes, which typically enhance faunal abundance and diversity (e.g. Orth et al. 1984; Mattila et al. 1999; Borg et al. 2010; González-Ortiz et al. 2016; our study) by regulating the availability of resources and providing shelter. Little is known about the relationships between *C. filum* and macrofauna, although gastropods have been documented in large clusters on *C. filum* (Pehrsson 1976). Most likely, *C. filum* was not a direct determinant driver for the macrofauna community in our seagrass sites, whereas it might be indicative of the presence of dense canopy meadows (Pehrsson 1976; our study) that dampen hydrodynamic forcing.

Physical or macrophyte characteristics are also explanatory variables for the macrofauna communities associated with seagrass (e.g. Orth et al. 1984; Frost et al. 1999; Mattila et al. 1999; Borg et al. 2010; González-Ortiz et al. 2016). Most of these studies focused on either the epifaunal or infaunal assemblages or specific species, and few studies encompassed the entire community (Boström et al. 2006b; Meysick et al. 2019). In our study, the variability of the epifauna community was better explained by macrophyte attributes (e.g. AGDM and algae), whereas the infaunal community was mainly explained by sedimentary predictors. Most of the epifauna species were highly mobile grazers (e.g. *Gammarus* spp, *Idotea* spp) that generally feed on epiphytic algae associated with seagrass blades (Mancinelli 2012; Boyé et al. 2017), and they are frequently associated with drifting algae (Norkko et al. 2000; Råberg and Kautsky 2007). Infaunal assemblages are typically linked to local sediment conditions (Gray 1974). However, infaunal species associated with seagrass meadows may be determined by macrophyte characteristics, including the belowground system (Frost et al. 1999; Boström et al. 2006a; González-Ortiz et al. 2016; Boyé et al. 2017; our study).

The variability of univariate macrofauna diversity indices (i.e. SR, and Shannon-Wiener index) was explained by a combination of sedimentary and macrophyte predictors, whereas macrofaunal community structure was better explained by sedimentary predictors. The variability of the macrofauna community was not exclusively linked to either

physical or biological mechanisms, but to a combination of different and interlinked drivers. For instance, the physical environment is a strong regulatory mechanism of seagrass communities, and simultaneously seagrass can modify the coastal physical environment by for instance trapping sediment particles and attenuating wave action (Bowden et al. 2001), facilitating macrofaunal SR (Meysick et al. 2019). Our results support the importance of considering a combination of different macrofauna descriptors, including the broad division into epifauna and infauna, to understand the mechanisms that regulate the variability of the seagrass macrofauna.

The role of drifting algal mats on the variability of the seagrass-associated macrofauna

The presence of drifting algae in our study explained the largest average contribution to the macrofauna community variability (>20%), particularly for the epifauna (34.2 and 40.5% of the abundance and biomass). Natural patches of algae are seasonally trapped in the aboveground complexity of vegetated meadows. High abundances of macrofauna, especially mobile epifauna such as amphipods and isopods, have been reported in sublittoral accumulations of drifting algae compared to bare sands and perennial vegetation communities (Holmquist 1994; Norkko et al. 2000; Råberg and Kautsky 2007). Our results provide empirical evidence that occurrences of drifting algae entangled among seagrass meadows can act as an alternative habitat for macroinvertebrates. Interestingly, the presence of drifting algae contributed to explaining a low but significant part of the variability of the infaunal biomass (5.4%). Most of the species collected with the benthic corer (especially molluscs such as *P. ulvae*) were opportunistic detritivore species (Table S10) that could benefit from the temporal presence of algal mats (Norkko et al. 2000). Furthermore, it is known that drift algae enhance dispersal of fauna among seagrass patches (Holmquist 1994; Brooks and Bell 2001). The dominance of the spatial turnover component in the β -diversity pattern emphasizes the high variability and complementarity of the seagrass meadows, reflecting a process of species replacement among sites that could benefit by the dispersal capacity of the drifting algal mats. Intense algal drifts caused by harmful algal blooms are known to inhibit the growth and survival of seagrass (McGlathery 2001; Gustafsson and Boström 2014). However, we showed that seasonally moderate drift mats made of heterogeneous algae have a positive effect on the diversity of the macrofauna community associated to the seagrass meadow.

Conclusions

Seagrass meadows are one of the most threatened marine habitats on earth, and preventing the loss of such complex and diverse habitat is a priority and a challenge for coastal conservation. Harmful algal blooms are considered one of the biggest threats to perennial vegetation in coastal habitats, and this poses a risk in the Baltic Sea due to global warming and a legacy of eutrophication leading to increasing amounts of algal mats drifting along the coastal habitats. However, the positive role of naturally occurring algal mats on the seagrass macrofauna has not been previously demonstrated. Understanding macrofauna community dynamics and the role of benthic biodiversity patterns across a seascape gradient of multispecific seagrass meadows is a priority, since the global scale of the biodiversity loss of coastal habitats calls for research studies to establish how biodiversity matters across

seascape scales and how it can respond to change. We emphasize the importance of considering different components of macrofauna community biodiversity in seagrass habitats, and in particular when using β -diversity patterns, to understand the processes driving species distribution that can guide practical management decisions.

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Data availability The manuscript has data included as electronic supplementary material.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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